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Corresponding Author: Dr. Irantzu Primicia,

Corresponding Author's Institution: Czech University of Life Sciences

First Author: Irantzu Primicia

Order of Authors: Irantzu Primicia; Jesús Julio Camarero; Juan Martínez de Aragón; Sergio de-Miguel; José Antonio Bonet

Abstract: Fungi provide important forest ecosystem services worldwide. In Mediterranean pine forests, predicted warmer and drier conditions could lead to a decline in mushroom yields. Climate is a key factor regulating both tree growth and fungal yields, particularly in drought-prone Mediterranean ecosystems. However, the responses of forest growth and mushroom production to climate depend on the differences among tree and fungal species and functional groups (e.g., mycorrhizal vs. saprotrophic), forest types, as well as depending on site conditions. Here we investigate how climatic conditions drive seasonal wood formation (earlywood –EW– and latewood –LW– production) and mycorrhizal mushroom production, to disentangle if growth and fungal yields are related. This assessment was done in Mediterranean forests dominated by four pine species in two areas located in Catalonia (NE Spain) representing mesic and xeric conditions and encompassing wide ecological gradients. The data consisted of 7-year to 13-year long inventories of mushroom production. EW production was favoured by cold and wet climate conditions during the previous fall and winter, and during the current spring and summer. LW production was enhanced by warm and humid conditions from spring to early fall. Mushroom yield was improved by wet late-summer and fall conditions, mainly in the most xeric area. This study confirms the ample differences found in tree growth and fungal production along ecological and climatic gradients. Clear relationships between mycorrhizal fungal yields and tree growth were mostly observed in specific sites characterized by severe summer drought. Specifically, latewood production seems to be the tree-ring variable most tightly linked to mycorrhizal fungal yield in drought-prone areas.

***Response to Reviewers**

Ms. Ref. No.: AGRFORMET-D-16-00082

Title: Linkages between climate, seasonal wood formation and mushroom yields Agricultural and Forest Meteorology

COMMENT:

The comments about the focus on edible mushrooms seems to be an important limitation to the general applicability of your study, I suggest to clearly indicate this in the title, or prominently in the abstract.

ANSWER:

Actually the yield data of all the fungi species (edible and non edible fungi) was included in the analysis. In our previous version of the manuscript it was described as follows "...and the collection included all epigeous ectomycorrhizal species as well as non-ectomycorrhizal edible species", what may have lead to some misunderstanding. Therefore, we have changed that sentence by "the collection included all sporocarps of all epigeous fungal species" (Page. 8, line 163) to specify that data of all fungi species have been included in the research.

Reviewers' comments
Reviewer #1:

COMMENT:

Manuscript entitled "Linkages between climate, seasonal wood formation and mushroom yields" represents and interesting approach to the knowledge of mushroom production and wood growth in relation with climatic parameters. Primicia and co-authors studied the effects of climatic conditions on seasonal wood formation and mushroom production in four different pine species of northeast Spain. They selected 19 plots in two sites where the meteorological conditions are different. The authors determined the climatic conditions that have a stronger influence on early and late wood formation as well as on mycorrhizal and saprotrophic yield. They also found an interesting relationship among latewood formation and mycorrhizal fugi production in the driest site.

In my opinion, the manuscript is adequate for the journal, matching with the journal focus, since it establishes the interrelationship between meteorology and vegetation and mushroom yield.

The data volume analyzed in this work and the amount of analyzes are impressive and the article is well organized and clear despite the huge amount of results presented. The methodology is clear and the results are intriguing and make ecological sense. I consider it as a valuable contribution.

Thus, I recommend the manuscript for publication in the journal. I just recommend some minor corrections, which I think could improve the excellent work made by the authors.

ANSWER:

We thank you for your positive comments on the manuscript.

Specific comments:

COMMENT:

Line 8.- Substitute the word saprophytic by saprotrophic for consistency with the rest of the manuscript.

ANSWER:

The highlight has been deleted as, after following the second reviewer's suggestion, the manuscript is now focused on mycorrhizal fungi.

COMMENT:

Line 138.- Spelling mistake: mushroom.

ANSWER:

Change done.

COMMENT:

Line 208.- If mushroom sampling was from September to December, why didn't you include December in mushroom production analyses?

ANSWER:

Change done. The relationships between mushroom yields and climate variables in December have been included (Fig. 4, Supplementary material Fig. A3).

COMMENT:

Lines 219-222.- I suggest using the scientific name of the *Pinus* species, in order to make it clearer for the reader.

ANSWER:

Change done.

COMMENT:

Line 402.- Bonet et al. 2008 is not in the listed references.

ANSWER:

Change done. The reference has been included in the reference list.

COMMENT:

Line 553.- Fig. A2. I think there is a mistake in the graph of *Pinus sylvestris* from Prades site for year 2012. Both bars are black and I suppose the one on the right should be gray. There is also a mistake in the y-axis title (year1-1). Yellow bars that indicate the production of saprotrophic species are difficult to appreciate.

ANSWER:

Changes done following the reviewer's suggestions. Yellow bars have been deleted as the manuscript is now focused on mycorrhizal fungi species.

Reviewer #3:

COMMENT:

Overall, it is a very good paper, but I have to *remark some aspe*cts that I think it will focus and improve the manuscript.

ANSWER:

We thank you for your positive comments on the manuscript.

COMMENT:

First, it is briefly mentioned that mushroom production considered to establish the linkages between climate, seasonal wood formation and mushroom yields is only that belonging to epigeous edible species (M&M line 175). This is a very important fact. Mushroom edibility is a criteria just based on socioeconomic traits, not about ecological relationships, so fungal yields are partially evaluated, moreover if it is considered that mushrooms are a minor representation of fungal presence/abundance in the ecosystems (considered a valid alternative by some authors). I think that this is a fundamental flaw, but data provided here by the authors have the greatest significance, due to the fact that long mushrooms production series are scarce over the world. This approach has limitations, so this fact (the only use of edible mushrooms) it must be clearly explained and stated along the manuscript.

ANSWER:

We agreed with the reviewer comment and edible yields has not been considered. Actually the yield data of all the fungi species (both edible and non edible fungi) was included in the analysis. In our previous version of the manuscript it was described as follows "...and the collection included all epigeous ectomycorrhizal species as well as non-ectomycorrhizal edible species", what may have lead to some misunderstanding. Therefore, we have changed that sentence by "the collection included all sporocarps of all epigeous fungal species" (Page. 8, line 163) to specify that data of all fungi species have been included in the research.

COMMENT:

Second, the main strength of this work is to establish the relation between climate, seasonal wood formation and mushroom yields, the three facts together. There are a lot of recent and old papers focusing linkage between climate and wood formation and climate and fungal yields. Results provided here agree with them. The novelty of the research is the connection between wood formation and fungal yields and those together with the climate, so this should be remarked in the Discussion Section (as it is done in the abstract).

ANSWER:

Change done. We have started the Discussion of the revised manuscript. emphasizing the main relationships found between climate and fungi production.

COMMENT:

Third, I think that the inclusion of data about saprotrophic fungi in this work does not increase its value. As it is very well explained in the Introduction Section, mycorrhizal fungi form symbiotic associations with host trees, which phenology and photosynthetic activity influence its development. Saprotrophic fungi do not form any association with those trees, so it is not expected any relationship between its yields and wood formation (explained in the main working hypotheses, fig. 1). In fact, Introduction section is focused only in mycorrhizal fungi. Authors focus Discussion Section on mycorrhizal mushrooms, stating that 'The production of the fruiting bodies of mycorrhizal fungi depends on the host photosynthetic rate, while the secondary growth is considered as a proxy of carbon availability to tree wood formation' (line 396).

I ask the authors that only use data from mycorrhizal fungi, analyzing data of total yields and mycorrhizal mushrooms, and changing title to 'Linkages between climate, seasonal wood formation and edible mycorrhizal mushroom yields'. It also has the greatest interest to include some of the conclusions in the title.

ANSWER:

Change done. We have used only data on mycorrhizal fungi in the manuscript, while some results on saprotrophic fungi yield have been moved to the supplementary material, as we think they are also interesting to readers. However, we have not included the relationships between climate and total fungi yield, because, as around 90 % of the total fungi yield was accounted by mycorrhizal fungi, the results between climate variables and mycorrhizal and total fungi yields are highly similar (And also related with the next reviewer comment about the excess of figures). Concerning the last comment, we have changed the title to “Linkages between climate, seasonal wood formation and mycorrhizal mushroom yields”.

COMMENT:

Fourth, there are a lot of figures. This mishandle the reader. Figures 3 to 7 should be provided like supplementary material and presented in the paper in a reduced version (maybe by tree species or by total results).

ANSWER:

We agree with your comment and, consequently, we have simplified and reduced the number of figures. We have deleted the Fig.1 of the previous version of the manuscript (working hypothesis) since, as we have deleted the hypothesis concerning saprotrophic fungi yields, we have simplified our main working hypothesis and that figure is no longer needed. However, we have kept most figures relating climate to tree-ring variables and fungi production as they are necessary to follow and understand the manuscript.

Linkages between climate, seasonal wood formation and mycorrhizal mushroom yields

HIGHLIGHTS

- Relationships between climate, wood formation and mycorrhizal fungi were analysed
- Climate signal varied among tree ring features and fungal functional guilds
- Mushroom yield mainly depended on summer water availability in the driest sites
- Latewood formation is linked with mycorrhizal fungal yield in dry sites

Linkages between climate, seasonal wood formation and mycorrhizal mushroom yields

Authors: Irantzu Primicia[a,b], J. Julio Camarero[c], Juan Martínez de Aragón[d], Sergio de-Miguel[e] and José Antonio Bonet[d,e]

[a]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, Praha 6–Suchdol, 16521 Prague, Czech Republic.
[b]Dpto. Ciencias del Medio Natural, Universidad Pública de Navarra, Campus de Arrosadía, Pamplona, Spain
[c]Instituto Pirenaico de Ecología (IPE-CSIC). Avda. Montañana 1005, 50059 Zaragoza, Spain
[d]Centre Tecnològic Forestal de Catalunya (CTFC-CEMFOR). Ctra. de St. Llorenç de Morunys km 2, E-25280 Solsona, Spain
[e]Departament de Producció Vegetal i Ciència Forestal, Universitat de Lleida-Agrotecnio Center (UdL-Agrotecnio), Avda. Rovira Roure, 191, E-25198 Lleida, Spain.

Email addresses: Primicia I. (irantzuprimicia@gmail.com)*, Camarero J.J. (jjcamarero@ipe.csic.es), Martínez de Aragón J. (mtzda@ctfc.es), de-Miguel S. (sergio.demiguel@pvcf.udl.cat), Bonet J.A. (jantonio.bonet@pvcf.udl.cat).

Corresponding author: Primicia, I.

Abstract

Fungi provide important forest ecosystem services worldwide. In Mediterranean pine forests, predicted warmer and drier conditions could lead to a decline in mushroom yields. Climate is a key factor regulating both tree growth and fungal yields, particularly in drought-prone Mediterranean ecosystems. However, the responses of forest growth and mushroom production to climate depend on the differences among tree and fungal species and functional groups (e.g., mycorrhizal *vs*. saprotrophic), forest types, as well as depending on site conditions. Here we investigate how climatic conditions drive seasonal wood formation (earlywood −EW− and latewood −LW− production) and mycorrhizal mushroom production, to disentangle if growth and fungal yields are related. This assessment was done in Mediterranean forests dominated by four pine species in two areas located in Catalonia (NE Spain) representing mesic and xeric conditions and encompassing wide ecological gradients. The data consisted of 7-year to 13-year long inventories of mushroom production. EW production was favoured by cold and wet climate conditions during the previous fall and winter, and during the current spring and summer. LW production was enhanced by warm and humid conditions from spring to early fall. Mushroom yield was improved by wet late-summer and fall conditions, mainly in the most xeric area. This study confirms the ample differences found in tree growth and fungal production along ecological and climatic gradients. Clear relationships between mycorrhizal fungal yields and tree growth were mostly observed in specific sites characterized by severe summer drought. Specifically, latewood production seems to be the tree-ring variable most tightly linked to mycorrhizal fungal yield in drought-prone areas.

Keywords: drought, tree growth, pine, forest, fungi, dendroecology.

Abbreviations: PS, *Pinus sylvestris*; PN *Pinus nigra*; PH, *Pinus halepensis*; PP, *Pinus pinaster*; EW, earlywood width; LW, latewood width; DBH, diameter at breast height; PET, potential evapotranspiration rate; P, precipitation; MFY, mycorrhizal fungi yield; CV, coefficient of variation.

1. Introduction

Climate plays a major role on the production and diversity of fungal communities, being precipitation, temperature and moisture key drivers for mushroom fruiting (Boddy et al., 2014; Pinna et al., 2010). In temperate and boreal forests, delayed fungal fruiting in fall or decreased fungal yield have been generally related to warmer and drier years, respectively (Kauserud et al., 2008; Diez et al., 2013). In Mediterranean pine forests, reduced mushroom yields usually correspond to more severe dryness during summer and autumn (Ágreda et al., 2015; Büntgen et al., 2015). Contrastingly, there is evidence of longer fruiting season and increased fungal production in temperate Central European forests due to rising temperatures (Büntgen et al., 2012, 2013). These diverse findings suggest that fungal yields are differently driven by climate depending on local site conditions (e.g., topography, soil properties) and forest stand dynamics (e.g., basal area, tree growth, Bonet et al., 2012, 2010, 2004; de-Miguel et al., 2014; Martínez-Peña et al., 2012; Tahvanainen et al., 2016). Nevertheless, when investigating fungal production as related to climate and forest growth, clear trends and associations between these three components are rarely observed, probably because of differences between functional fungal groups, forest types, climatic conditions and methodological issues affecting fungal records (Boddy et al., 2014).

The symbiotic associations formed by mycorrhizal fungi with tree roots enhance the transfer of soil nutrients to trees, while organic carbon compounds fixed by trees are derived to fungi (Gerdemann, 1970). The phenology and photosynthetic activity of the host tree and its response to climate may also influence differently mycorrhizal and saprotrophic fungal fruiting arising from their differential dependence on climate conditions (Boddy et al., 2014). Additionally, the sensitivity of mycorrhizal fungi to climate may depend on the tree-fungi associations and the strength of those relationships (e.g. deciduous *vs*. coniferous tree species, Gange et al., 2007). Nevertheless, links between the type of tree host species and the phenology of mushroom fruiting have been detected in some cases (Dickie et al., 2010) whilst in others no association has been found (Pinna et al., 2010).

Tree radial growth may be used as a proxy of carbon availability to trees since wood formation has a low allocation priority compared to shoot development (Fritts, 2001). The study of tree-ring features for ecological purposes (dendroecology) is therefore a powerful tool to understand how coupled long-term climatic conditions, forest growth, and mushroom production are (Büntgen and Egli, 2014). Mycorrhizal fungal production has been indeed associated with tree growth in thinning experiments (Egli et al., 2010). However, since the production of mushroom fruiting bodies is apparently highly dependent on current photosynthates (Högberg et al., 2008), mycorrhizal mushroom yield could be related to seasonal wood production as, in conifers, the latewood is mostly formed by current-year photoassimilates, while the earlywood contains carbohydrates synthesized from the previous summer and fall and current spring (Kagawa et al., 2006). Therefore, observational studies aiming to relate climate, wood and mycorrhizal fungal production should consider the main climatic constraints of tree growth and fungal fruiting, and the phenological patterns of both processes which are linked to carbon synthesis and use within the tree. For example, these studies should consider that both mycorrhizal mushroom production and latewood formation usually peak during summer and autumn in most conifers of the Northern Hemisphere and therefore, these two variables could be coupled to some degree.

In this framework, we propose assessing the potential of tree rings to investigate the long-term relationships between climate conditions, seasonal wood formation (earlywood and latewood widths), and mycorrhizal mushroom production. We argue that mycorrhizal and saprotrophic fungal production during fall, when maximum yields are recorded in the Northern Hemisphere, must be separately considered based on their different dependence on climate (Egli et al., 2010). Our main objectives are (1) to determine the main climate variables influencing seasonal wood formation and mycorrhizal fungal productions, and (2) to analyse whether the production of mycorrhizal fungi is related to earlywood and latewood production. Our working hypothesis are that: (1) earlywood formation will be influenced by spring climatic conditions whilst latewood formation will be more dependent on late-summer and fall climate; (2) annual mycorrhizal fungi yields will be mainly influenced by late-summer and fall climate conditions,

when fungi fruiting peaks; (3) the influence of water availability on both wood (earlywood and latewood widths) and mycorrhizal mushroom production will be stronger in the most xeric sites; and (4) latewood width, and not earlywood production, will be related to mycorrhizal fungi yield as a function of late summer to fall climatic conditions.

2. Material and Methods

2.1. Study area

The study was conducted in monospecific stands of the most common pine forest ecosystems found in Catalonia, NE Spain (*Pinus sylvestris* L., *Pinus nigra* J.F. Arnold, *Pinus halepensis* Mill. and *Pinus pinaster* Ait.). We selected two areas subjected to different climatic conditions (Solsonès and Prades) for sampling (Fig. 1). The plots in Solsonès area corresponded to natural stands, whereas the Prades plots were placed on pine plantations established in the 1960s. Of the total of 107 permanent plots currently monitored for the annual mushroom yield estimation (de-Miguel et al., 2014), we sampled nineteen stands (13 stands in Solsonès and 6 stands in Prades) located between 530 and 1502 m a.s.l., corresponding to highly productive fungal areas (Table 1). Therefore, total mushroom yields from the selected sample plots need to be considered with care inasmuch as they may not be necessarily representative of the expected productivity of a typical forest stand.

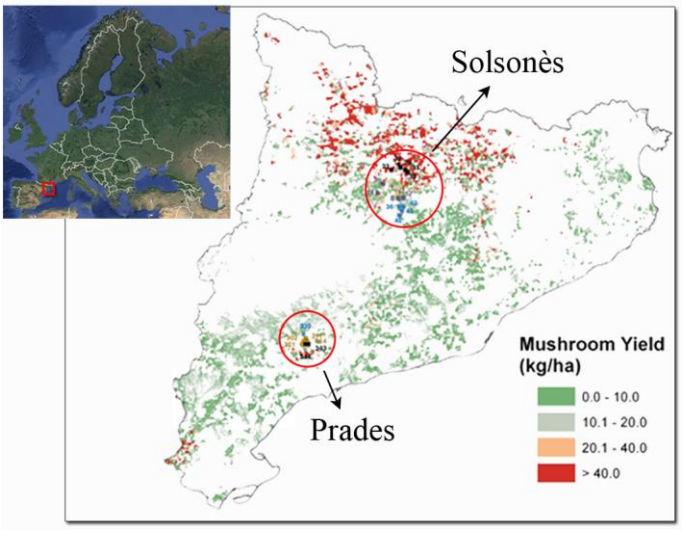


Figure 1. Map of mean annual mushroom yields obtained for Catalonia showing its location within Europe and the sampled sites in the Solsonès and the Prades study areas (Adapted from Bonet et al., 2014).

The Solsonès area is subjected to continental and sub-Mediterranean conditions, with a mean annual temperature of 11.1 ºC and a mean annual precipitation of 726 mm, whereas the Prades area experiences a stronger Mediterranean influence, i.e. a more intense drought stress during the growing season (mean annual temperature of 12.1 ºC and mean annual precipitation of 564 mm). For each plot, physiographic and stand attributes such as slope, aspect, elevation, tree density and basal area were also recorded (cf. Table 1).

Table 1. Summary of the plot characteristics data and mushroom yield (fresh weight) measured in Catalonian pine forests, NE Spain. Values of stand variables are means (ranges are given between parentheses).

Site	Pine species (code)	No. sampled plots	Period of fungi data (No. years)	Tree density (No. trees ha^{-1})	Stand basal area (m^2 ha^{-1})	Altitude (m a.s.l.)	Aspect (º)	Slope (%)	Mushroom yield (kg ha^{-1} yr^{-1})		
									Mycorrhizal fungi	Saprotrophic fungi	Total
Solsonès	*P. sylvestris*, Scots pine (PS)	5	1997-2001 (5) 2007-2014 (8)	1453 (552 - 3893)	21.1 (11.1 - 30.2)	1033 (854 - 1502)	156 (63 - 282)	24 (17 - 33)	79.1 (0 - 286.5)	2.4 (0 - 20.4)	81.5 (0.2 - 307)
	P. nigra, Black pine (PN)	4	1997-2001 (5) 2007-2014 (8)	1613 (1100 - 2292)	26.2 (15.3 - 41.7)	773 (630 - 1040)	188 (14 - 317)	11 (5 - 19)	105.1 (0 - 472.7)	2.6 (0 - 21.4)	107.8 (0 - 474.7)
	P. halepensis, Aleppo pine (PH)	4	1997-2001 (5) 2007-2014 (8)	1905 (281 - 3883)	24.2 (16.4 - 31)	613 (530 - 661)	243 (170 - 292)	16 (10 - 34)	38 (0 - 281.2)	4.2 (0 - 63.6)	42.2 (0 - 293.2)
Prades	*P. sylvestris*, Scots pine (PS)	2	2008-2014 (7)	1066 (541 - 1592)	49.7 (48.3 - 51.1)	853 (841 - 864)	325 (310 - 340)	13 (8 - 18)	228.5 (0 - 551.2)	21.4 (0 - 87.3)	249.9 (2 - 638.5)
	P. pinaster, Maritime pine (PP)	4	2008-2014 (7)	1088 (446 - 2552)	40.6 (21 - 80.3)	807 (594 - 1013)	154 (10 - 360)	13 (3 - 22)	79.1 (0 - 450.7)	17.3 (0 - 81)	96.4 (0.2 - 481.6)

2.2. Data collection

2.2.1. Dendrochronological methods

Around each plot where mushroom production was assessed, 10-15 dominant trees were randomly selected for sampling in late 2014 and early 2015 in an area *ca*. 0.5-ha large. Two radial cores per tree were extracted at 1.3 m above the ground level using a Pressler increment borer. The cores were air-dried, mounted on wood boards, and polished with sandpaper grits until rings were clearly visible. The wood samples were visually cross-dated. Then, earlywood (EW) and latewood (LW) widths were separately measured to the nearest 0.01 mm using a stereomicroscope and a Lintab sliding-stage measuring device in conjunction with TSAP-WinTM software (F. Rinn, Heidelberg, Germany). EW and LW were visually distinguished based on the different lumen area and cell-wall thickness of the tracheids forming each type of wood. Cross-dating was verified using the COFECHA program (Holmes, 1983). We obtained chronologies of EW and LW widths for each plot by averaging the values for each year across the trees sampled within each plot. For each tree, we measured the diameter at breast height (DBH) and estimated the age at 1.3 m by counting the number of rings of the oldest core containing the pith or showing the innermost curved rings indicating proximity to the pith.

2.2.2. Mushroom yield assessments

Mushroom sampling started in 1997 in Solsonès plots, and in 2008 in Prades plots. From 2002 to 2006, sampling was not carried out. Mushroom production (fresh mass) and species richness were inventoried every week from September to December in squared plots (10 m x 10 m), when most fungi fruiting occurs (Bonet et al., 2012; Martínez de Aragón et al., 2007), and the collection included all sporocarps of all epigeous fungal species. All collected sporocarps were identified at the species level whenever possible, even though some samples could only be identified to higher taxonomic levels. Additional information on the sampling methodology can be found in Bonet et al. (2012, 2010), de-Miguel et al. (2014) and Martínez de Aragón et al. (2007).

2.2.3. Climate data

Monthly climatic variables (minimum, maximum and mean temperatures, and total precipitation) were obtained for the 1970-2014 period from the E-OBS gridded dataset by selecting the 0.25º grids including the two sampling sites (Haylock et al., 2008). We used these gridded data because they were similar and more updated than other climatic data obtained from interpolated Spanish databases at a finer spatial resolution (Supplementary Material, Fig. A1).The potential evapotranspiration rate (PET) at each plot was estimated following Hargreaves and Samani (1982) and using monthly minimum and maximum temperature using the *SPEI* package (Vicente-Serrano et al., 2010, Beguería et al., 2014) in the R software (R Core Team, 2015). The water balance was calculated afterwards as the difference between mean monthly precipitation and PET.

2.3. Statistical analyses

The mean EW and LW series obtained for each study plot were correlated against monthly minimum and maximum temperature, precipitation (P) and water balance (P-PET) using bootstrapped Pearson correlation coefficients on a 13-month window from September of the year prior to tree growth until October of the year of tree-ring formation. This window encompasses the period climatically most relevant for pine growth in the study area (Camarero et al., 2010). The statistical significance of the correlations was tested using the 95% percentile range method and taking into account the presence of temporal autocorrelation in the EW and LW series (Dixon, 2001). Note that we used raw EW and LW data and not detrended and prewhitened indices because: (i) both variables did not show significant trends during the period when overlapped with fungi yield data (1997-2014), and (ii) we aimed to preserve year-to-year EW and LW variability which could be related to fungi production. We used Spearman correlation, which is a non-parametric and robust rank statistic suitable for non-linear associations, to analyse the response of mean annual mushroom production (mycorrhizal and saprotrophic fungi yields) quantified as fresh mash (kg ha^{-1} $year^{-1}$) to the abovementioned climate variables from January to December.

Spearman correlation was also used to assess the relationships between mean annual mycorrhizal fungi yield (MFY) and EW and LW. We also performed partial Spearman correlations between LW and MFY controlling for climatic (cumulative precipitation from August to September) and growth effects (EW production). We investigated if the correlations between EW and LW, and MFY were modulated by the plots characteristics using linear regressions. All statistical analyses were conducted using the R statistical software (R Core Team, 2015).

3. Results

3.1. Tree growth patterns and responses to climate

Both EW and LW widths were highly variable among tree species and sites (Table 2), with highest values in the Prades *Pinus pinaster* (PP) and the Solsonès *P. sylvestris* (PS) plots, followed by the Prades PS plots, and finally, by the *P. halepensis* (PH) and the *P. nigra* (PN) plots in Solsonès area. The proportion of LW ranged from 9 to 72%, with a mean value of 28%.

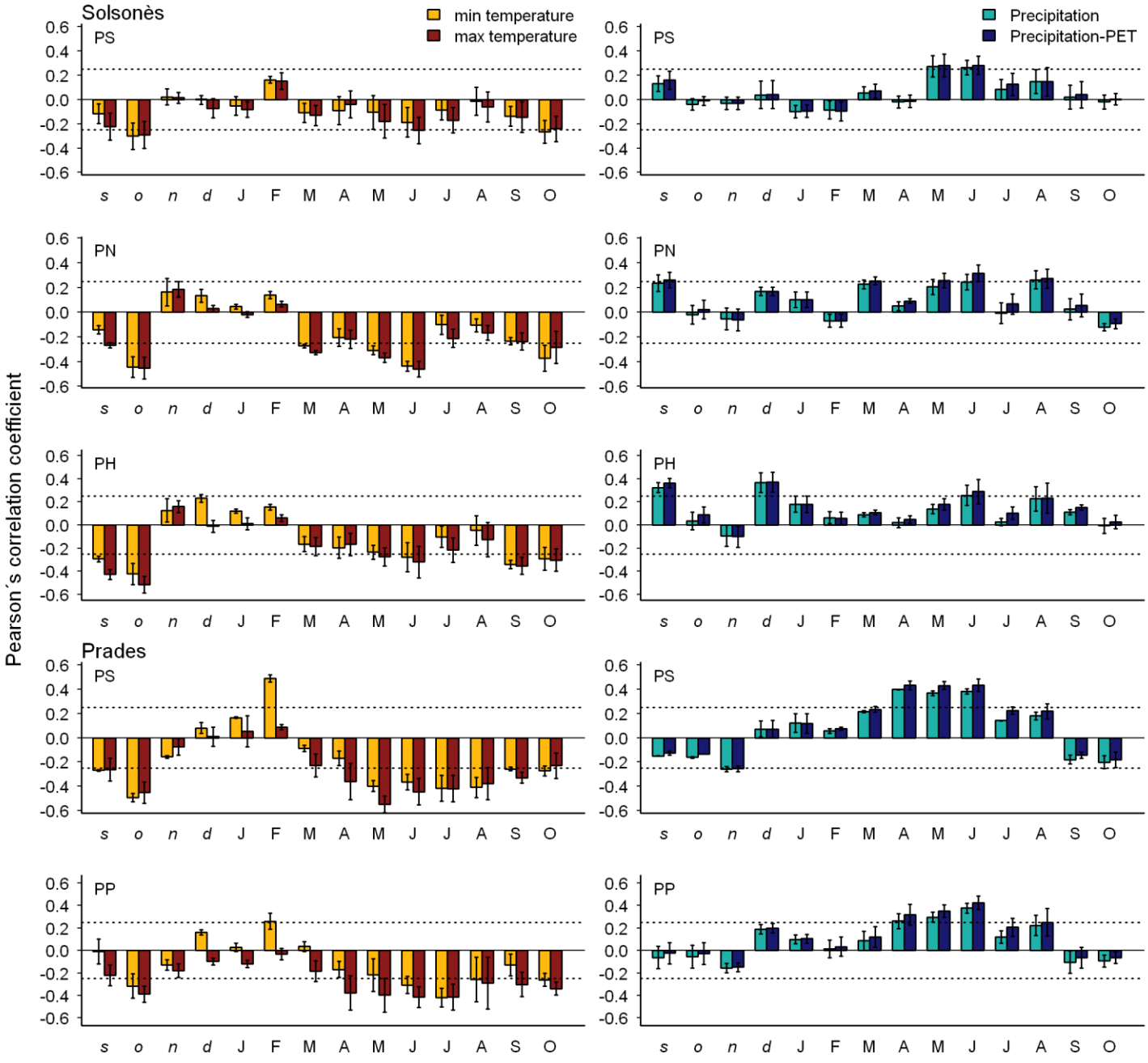
Table 2. Descriptive statistics (age, diameter at breast height- DBH, correlation with the mean series of each forest, earlywood width- EW, and latewood width- LW) for the tree-ring width chronologies of each study plot. Values are means ± SD.

Site	Pine species	Plot	Age	DBH (cm)	Correlation with Master	Mean EW for the period 1990-2014 (mm)	Mean LW for the period 1990-2014 (mm)
Solsonès	Scots pine (PS)	PS029	70 ± 7	11.8 ± 2.9	0.54	0.7 ± 0.4	0.2 ± 0.2
		PS030	73 ± 9	12.4 ± 1.9	0.53	0.7 ± 0.3	0.5 ± 0.3
		PS031	33 ± 4	11.4 ± 3.2	0.81	0.6 ± 0.4	0.3 ± 0.3
		PS032	63 ± 7	15.9 ± 2.8	0.61	0.6 ± 0.2	0.3 ± 0.2
		PS033	42 ± 13	17.9 ± 7.7	0.67	0.6 ± 0.2	0.3 ± 0.2
	Black pine (PN)	PN008	78 ± 6	15.5 ± 2.7	0.71	0.6 ± 0.2	0.3 ± 0.2
		PN009	48 ± 3	11.6 ± 2.1	0.73	0.5 ± 0.1	0.2 ± 0.2
		PN011	76 ± 5	14.0 ± 2.2	0.67	0.4 ± 0.2	0.2 ± 0.2
		PN017	93 ± 26	14.6 ± 4.2	0.71	0.9 ± 0.3	0.4 ± 0.1
	Aleppo pine (PH)	PH036	78 ± 17	18.9 ± 5.6	0.72	1.0 ± 0.3	0.3 ± 0.1
		PH040	76 ± 13	13.2 ± 2.2	0.63	1.8 ± 0.7	0.6 ± 0.4

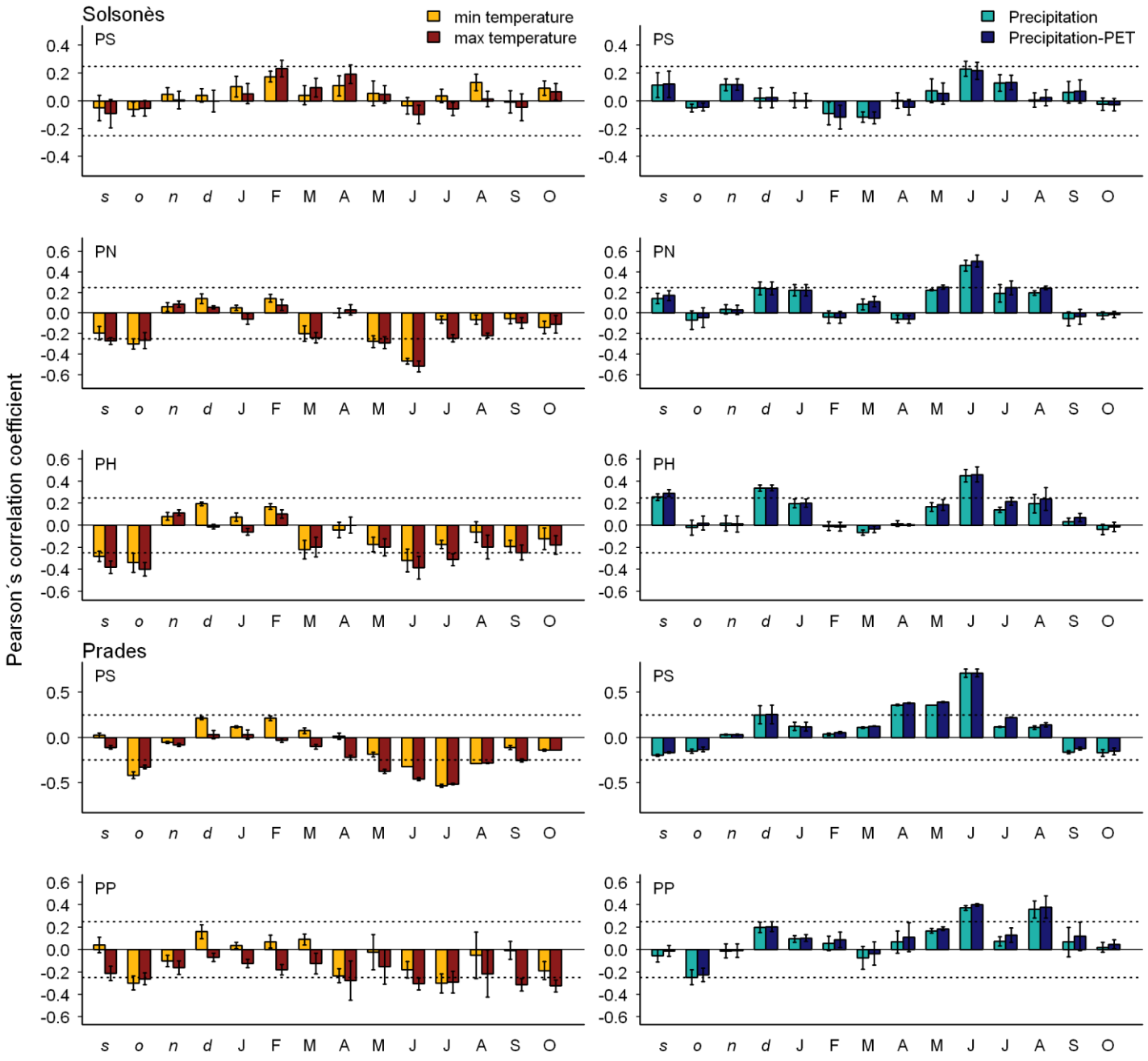
		PH041	64 ± 21	14.7 ± 3.0	0.63	1.2 ± 0.4	0.4 ± 0.3
		PH042	87 ± 13	15.3 ± 3.0	0.67	0.6 ± 0.1	0.2 ± 0.1
Prades	Scots pine (PS)	PS343	53 ± 3	16.6 ± 2.7	0.71	0.6 ± 0.1	0.2 ± 0.1
		PS344	116 ± 24	20.0 ± 4.8	0.57	1.1 ± 0.5	0.5 ± 0.4
	Maritime pine (PP)	PP301	41 ± 3	17.3 ± 2.8	0.66	0.9 ± 0.4	0.4 ± 0.2
		PP302	40 ± 2	16.6 ± 2.5	0.79	1.5 ± 0.5	0.6 ± 0.2
		PP311	35 ± 6	17.1 ± 2.3	0.76	0.7 ± 0.1	0.4 ± 0.1
		PP314	64 ± 7	20.2 ± 3.1	0.62	0.6 ± 0.1	0.2 ± 0.1

EW was more sensitive to climate conditions than LW (Figs. 2 and 3). The response of EW to climate varied among tree species and study areas, except for warm conditions during September and October of the previous year, which generally reduced the EW production (Fig. 2). EW frequently responded negatively to warm temperatures from current May to June and from September to October in Solsonès, and from April to September- October in Prades. Additionally, EW was enhanced by higher minimum temperature values in February in the Prades plots. The sensitivity of EW to humid conditions in May- June increased towards the more xeric sites (Prades), where humid conditions in April were also important. The response of EW to climate variables was site-specific. Thus, while PS pines from Prades showed an EW negative response to warm conditions from April to October, in Solsonès, growth of this species was not affected by temperature during the year of tree-ring formation.

Warm temperatures during September and October of the previous year generally reduced LW, except in the Solsonès PS plots (Fig. 3). LW also decreased with warm conditions: from May to June in Solsonès PN plots; during June, July and September in Solsonès PH plots; from May to September in Prades PS plots; and in April, June, July, September and October in Prades PP plots. In Solsonès PN and PH plots, LW was enhanced by humid conditions in previous December and current June. In Prades, LW increased with increasing water availability in previous December and from April to June in PS plots, and in June and August in PP plots. Again, Prades PS plots were more sensitive to climate variables in terms of LW formation than those located in the less xeric Solsonès area.



238 **Figure 2.** Correlations (Pearson coefficients) obtained by relating earlywood width and
239 minimum and maximum temperatures, precipitation, and water balance (precipitation minus
240 potential evapotranspiration, PET). Months abbreviated by lowercase or uppercase letters
241 correspond to months from the previous and current years, respectively. Horizontal dashed lines
242 represent $P < 0.05$ significance levels. Pine species abbreviations are as in Table 1.
243



244 **Figure 3.** Correlations (Pearson coefficients) obtained by relating latewood width and minimum
245 and maximum temperature, precipitation, and water balance (precipitation minus potential
246 evapotranspiration, PET). Horizontal dashed lines represent $P < 0.05$ significance levels. Rest of
247 explanations are as in Figure 2.

248

249 ### 3.2. Influence of climate on mushroom yields

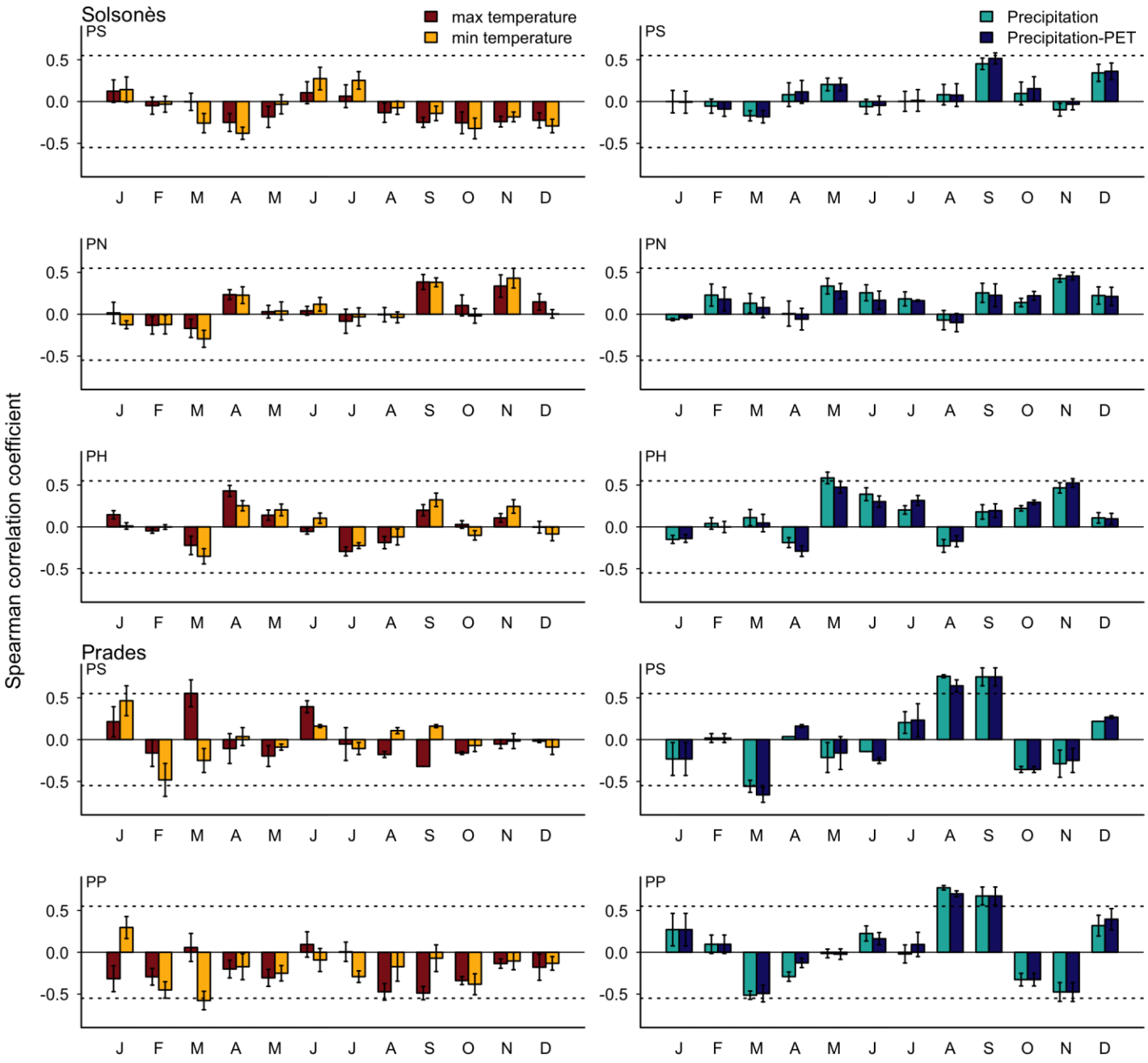
Mushroom production was highly variable among years (coefficient of variation, CV = 83.1 %) and plots (CV = 68.6 %). Annual mycorrhizal fungi yield (MFY) accounted for over than 90 % of the total fungi yield. Mean MFY was 85.3 kg ha^{-1} yr^{-1}, the values ranging from 0 to 551.2 kg ha^{-1} yr^{-1}, while the annual saprotrophic fungi yield averaged 6.1 kg ha^{-1} yr^{-1} and ranged from 0 to 87.3 kg ha^{-1} yr^{-1}. The highest mushroom yields were recorded in Prades PS plots (*ca.* 230 kg ha^{-1} yr^{-1}), with maximum yearly productions exceeding 500 kg ha^{-1} yr^{-1} (Table 3). Years 2000, 2008, 2010, and particularly, 2014, were characterized by a high production of mycorrhizal fungi, whilst years 1997, 2009 and 2013 were characterized by low fungi yields (Supplementary Material, Fig. A2). The study plots show a high fungal diversity, having collected more than 110 different mycorrhizal species in one Scots pine plot (Supplementary Material, Table A1).

Table 3. Mean, maximum and minimm mycorrhizal and saprotrophic fungal yield per plot (kg ha^{-1} $year^{-1}$) and total number of mycorrhizal and saprotrophic identified species per plot. Pine species abbreviations are as in Table 1.

Site	Pine species	Plot	Mycorrhizal fungi			Saprotrophic fungi		
			Mean yield (kg ha^{-1} $year^{-1}$)	Max-Min yield (kg ha^{-1} $year^{-1}$)	No. species	Mean yield (kg ha^{-1} $year^{-1}$)	Max-Min yield (kg ha^{-1} $year^{-1}$)	No. species
Solsonès	PS	PS029	62.6	163.6-6.6	56	0.6	6.4-0.0	12
		PS030	48.1	170.5-0.0	74	1.4	9.5-0.0	32
		PS031	94.4	216.4-2.4	54	4.5	19.5-0.0	20
		PS032	91.3	207.8-4.5	114	1.1	5.7-0.0	30
		PS033	99.1	286.5-0.2	86	4.6	20.4-0.0	46
	PN	PN008	29.8	214.4-0.0	47	4.3	21.4-0.0	29
		PN009	185.6	472.7-11.4	81	2.6	10.9-0.0	43
		PN011	112.9	383.8-0.0	74	3.1	10.7-0.0	38
		PN017	92.2	349.6-0.4	52	0.6	3.0-0.0	26
	PH	PH036	8.0	35.2-0.0	30	0.4	2.8-0.0	16
		PH040	59.3	222.4-0.0	64	3.7	18.0-0.0	41
		PH041	20.1	135.5-0.0	42	10.1	63.6-0.0	40
		PH042	64.7	281.2-0.0	61	2.6	14.8-0.0	22
Prades	PS	PS343	231.7	538.9-0.0	58	19.6	56.4-0.5	29
		PS344	225.3	551.2-0.0	68	23.2	87.3-0.0	29

PP	PP301	73.4	267.8-0.0	35	15.3	31.3-0.1	31
	PP302	69.3	159.0-0.0	30	39.1	81.0-1.0	26
	PP311	128.2	450.7-0.6	23	11.6	30.9-0.2	42
	PP314	84.5	238.6-0.0	54	11.5	23.1-2.2	35

The influence of climate on fungal yield differed among functional guilds, tree species, and sites (Fig. 4). Thus, the production of saprotrophic fungi was more sensitive to climate conditions than the MFY under the more xeric conditions (Supplementary Material, Fig. A3). In Solsonès, MFY was significantly influenced by precipitation values in May in the PH plots (positive relationship, Fig. 4). In Prades, MFY was enhanced by high values of maximum temperature in March in the PS plots, but it was reduced by high values of minimum temperatures during the same month in the PP plots. Additionally, MFY was improved by humid conditions in August and September in both PS and PP plots, while it was negatively related to precipitation and water balance during March in the PS plots. The response of MFY to climate variables in the PS plots changed between sites (e.g. the positive influence of humid conditions during summer on MFY in PS plots was only observed in the more xeric Prades area).

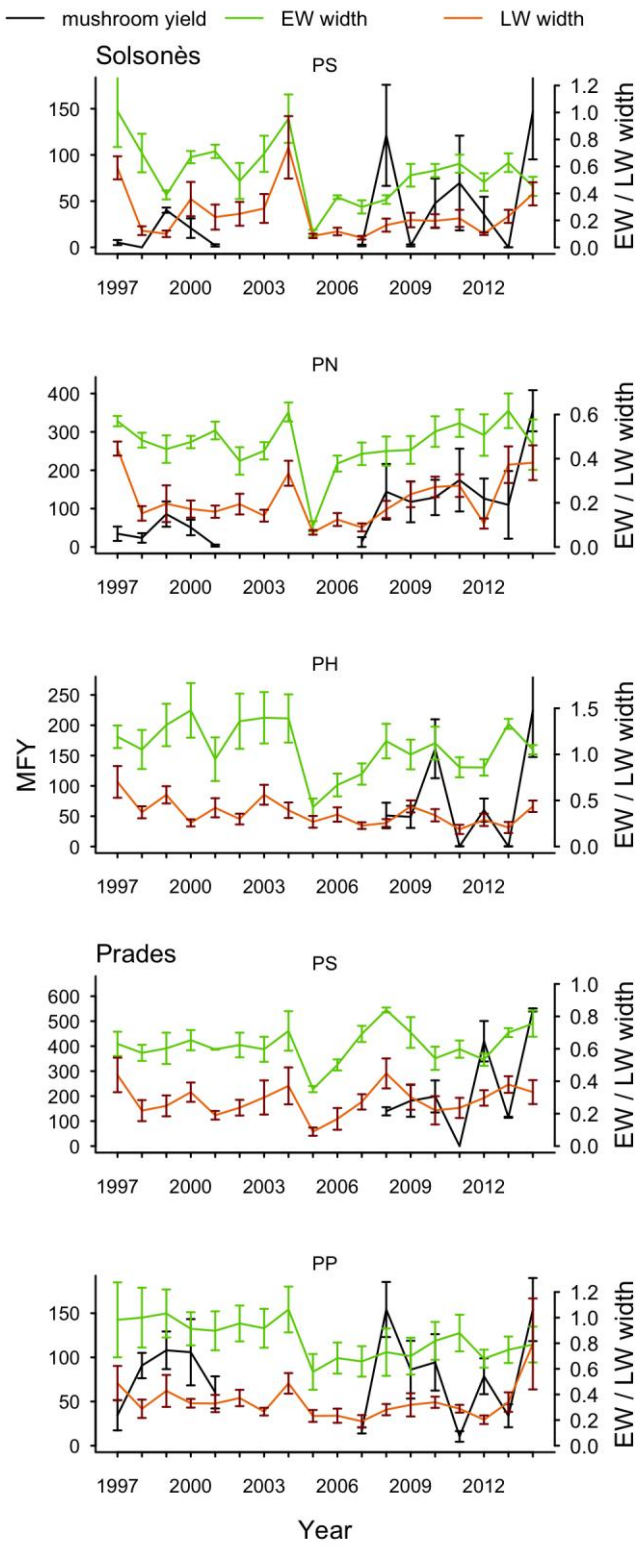


279 **Figure 4.** Correlations (Spearman coefficients) obtained by relating annual mycorrhizal fungi
280 yield and monthly minimum and maximum temperature, total precipitation, and water balance
281 (precipitation minus potential evapotranspiration, PET) for each pine species and sample site.
282 Horizontal dashed lines represent $P < 0.05$ significance levels. Pine species abbreviations are as
283 in Table 1.

284

285 **3.3. Linkages between mycorrhizal mushroom production and tree growth**

In general, no clear temporal coupling was observed between mean annual mycorrhizal fungi yields and EW and LW production excepting for some sites (Fig. 5). Significant relationships between MFY and EW were only found in the Solsonès area, where both negative (some PN and PS plots) and positive (one PN plot) relationships were observed (Table 4). Mycorrhizal fungi yield was related to LW production only in some Prades PP plots (positive associations). When controlling for the main climatic constraints of tree growth (cumulative precipitation from August to September), significant and positive LW-MFY correlations were found for two PP plots in Prades. When controlling for growth effects of EW on LW, positive LW-MFY correlations were observed in Prades (both PP and PS plots) and in some PH and PN plots in Solsonès. Regarding site conditions, correlations and partial correlations between LW and MFY increased when the plot slope decreased (Supplementary Material, Fig. A4).



298 **Figure 5.** Temporal trends of mean annual mycorrhizal (MFY) fungi yields (left y axes, fungi
299 production data are fresh mass in kg ha^{-1} $year^{-1}$) and earlywood (EW) and latewood (LW)
300 widths (right y axes, data are in mm). Values are means ± SE. Pine species abbreviations are as
301 in Table 1.

Table 4. Spearman correlations calculated between earlywood (EW) and latewood widths (LW) and mean annual mycorrhizal fungi yield (MFY). Partial correlations were also calculated between LW and MFY controlling for climatic (cumulative precipitation from August to September) or growth effects (EW). Pine species abbreviations are as in Table 1. Significance levels: *0.05< $P \leq 0.1$; **0.05< $P \leq 0.01$; ***0.01< $P \leq 0.001$

Site	Pine species	Plot	No. years of data	EW *vs.* MFY	LW *vs.* MFY	Partial correlations	
						LW *vs.* MFY controlled for precipitation	LW *vs.* MFY controlled for EW
Solsonès	PS	29	13	0.44	0.37	0.33	0.09
		30	13	-0.55*	-0.07	-0.12	0.34
		31	13	0.13	0.07	-0.16	0.01
		32	13	-0.23	-0.30	-0.37	-0.21
		33	13	-0.24	0.15	0.06	0.31
	PN	8	13	-0.59*	0.21	0.14	0.52*
		9	13	0.58*	0.47	0.48	0.31
		11	13	-0.05	0.48	0.51	0.53*
		17	13	-0.59*	0.04	0.02	0.58*
	PH	36	13	-0.49	-0.41	-0.47	-0.25
		40	13	-0.11	0.19	0.19	0.32
		41	13	-0.35	0.09	0.04	0.34
		42	13	-0.25	0.40	0.43	0.63**
Prades	PS	343	7	-0.07	0.04	-0.59	0.13
		344	7	0.11	0.43	-0.39	0.74*
	PP	301	6	0.33	0.64	0.07	0.69
		302	7	-0.36	0.71	0.61	0.85***
		311	7	0.18	0.75*	0.85**	0.76**
		314	7	-0.11	0.82*	0.79***	0.85***

4. Discussion

The novelty of this research is the described connection between wood formation and fungal yields, and characterizing how this link depends on climate variability. The climate signal on tree-ring features and mushroom productivity varied among host tree species and increased towards the drier sites. In the study sites subjected to the driest summer, mycorrhizal fungal yields increased in response to wet late-summer to fall conditions. These climatic

316 conditions also favoured latewood formation, which explains why latewood production
317 correlated to mycorrhizal fungal yield in such drought-prone sites.
318
319 **4.1. Tree growth responses to climate**
320 Additionally to our first hypothesis (EW and LW mainly driven by climate conditions in
321 spring and in late-summer and fall, respectively), both EW and LW were influenced by climate
322 conditions during previous fall and from April to October. EW was more sensitive to climate
323 variability than LW, agreeing with previous findings in other Mediterranean pine forests (Pasho
324 et al., 2012). EW formation was enhanced by cold and wet climate conditions during the
325 previous fall and winter, and current spring and summer. LW responded to temperature
326 (negatively) and precipitation (positively) from spring to early fall indicating that wet and cool
327 conditions during the late growing season favour carbon use in radial growth and tracheid cell-
328 wall thickening and lignifications, as it has been also observed in Corsican pine stands in
329 western France (Lebourgeois, 2000). The responses of both EW and LW to climate were site
330 and species specific, showing an increasing influence of summer conditions in the more xeric
331 sites subjected to Mediterranean conditions (Prades study area).
332
333 **4.2. Mycorrhizal mushroom production and its response to climate**
334 In the more xeric Prades study area, mycorrhizal fungi were less climate-dependent than
335 saprotrophic fungi, as it has been already described previously (Boddy et al., 2014; Diez et al.,
336 2013). Due to the symbiotic associations with tree roots, the mycelium of mycorrhizal fungi
337 may explore deeper soil layers than the saprotrophic fungi mycelium, which mainly occupies
338 the organic soil layer (Diez et al., 2013). Additionally, the ecology of mycorrhizal fungi is
339 influenced by the fungi-tree interactions (e.g. transfer of nutrients and carbohydrates between
340 trees roots and fungi in the rizosphere; Boddy et al., 2014), and by the performance of trees (e.g.
341 leaf and root phenology, photosynthetic activity and carbon use). For instance, water may be
342 transferred from the hosts to their mycorrhizal simbionts in response to drought stress
343 (Querejeta et al., 2003). Therefore, the production of mycorrhizal fungi may be expected to rely

344 less on climate conditions than saprothrophic fungi, even though similar direct climate controls
345 on the fruit body production of both functional guilds have been also suggested (Büntgen et al.,
346 2013).

347 The different response of fungi production to climate among the species *x* site
348 combinations were probably related to elevation-induced changes in the local climate conditions
349 (Pinna et al., 2010). Thus, the higher sensitivity of mushroom production to summer
350 precipitation observed in the Scots pine plots located in Prades (elevational range: 841 – 864 m)
351 than those in Solsonès (elevational range: 854 – 1502 m) might have been related to to a higher
352 drought stress in Prades sites linked to lower elevation. Indeed, previous studies suggest that
353 temperature influences fungal activity under humid climate regimes, while water availability
354 gains importance towards drier sites (e.g. Bonet et al., 2010; Büntgen et al., 2012; de-Miguel et
355 al., 2014). Accordingly, de-Miguel et al. (2014) discussed that mushroom production may
356 decrease towards higher elevations because of low temperature constraints, even though water
357 availability increases. However, in our study, mushroom production was not apparently
358 restricted by low temperatures in the Scots pine plots located in the mesic Solsonès area,
359 probably because there were not plots in temperate or precipitation- limited conditions and also,
360 due to the limitation of the climatic data used in this study, being assigned the same climatic
361 data to all the Solsonès plots.

362

363 **4.3. Linkages between mycorrhizal mushroom production and seasonal wood formation**

364 Mycorrhizal mushroom yield was frequently coupled with latewood width production,
365 particularly in sites under severe summer drought conditions. The production of mycorrhizal
366 fruiting bodies is highly dependent on the transfer of current photosynthates from the tree to the
367 fungi (Högberg et al., 2008). Thus, disturbances which reduce that photosynthates transfer such
368 as defoliation have been found to affect ectomychorrhizal fungi fruiting (Kuikka et al., 2003).

369 Tree secondary growth could be therefore expected to be associated with mycorrhizal
370 fungi fruiting if carbon allocation rates to roots and stem wood are tightly related. In this
371 framework, the production of ectomycorrhizal fruiting bodies has been suggested to increase

with the photosynthetic capacity of the associated trees (Egli et al., 2010), while when studying plots covering a range of stand basal areas, mushroom production is maximum when the annual increment of the stand basal area peaks (Bonet et al., 2010, 2008). Tree growth-fungi fruiting relationships have been previously investigated in thinning experiments, but contrasting responses of mycorrhizal fungi yield after thinning have been obtained (e.g. Bonet et al., 2012; Egli et al., 2010; Pilz et al., 2006). Additionally, cautious should be taken when investigating growth- fungi associations after thinning since fungi yields may also depend on the season, pattern and intensity of the thinning (Egli et al., 2010; Luoma et al., 2004).

Based on an in-vitro experiment, Fortin et al. (2008) suggested that the onset of the mushroom season occurs when the terminal buds of associated trees are developed at the beginning of fall, when the mobile carbon pool in the roots is nearly twice than in spring (Li et al., 2002). Furthermore, in conifers current-year photoassimilates are mainly used in latewood formation, while carbohydrates synthesized from the previous summer and fall and current spring are mainly involved in earlywood formation (Kagawa et al., 2006). Consequently, we hypothesized that mycorrhizal fungi production during fall could be linked to latewood width rather than with earlywood or tree-ring width. According to that hypothesis, we did find positive and significant relationships between mycorrhizal fungi production and latewood width, the number of these relationships being highest when controlling for the growth effects on the latter. Significant associations were freqently found in PN plots in Solsonès and PP plots in Prades, probably related to the carbon use within trees and water limitations during the growing season, as it has been already suggested by Büntgen et al. (2015). They found similar responses between mycorrhizal fungi production and latewood width in a Scots pine forest located in Central Spain under Mediterranean and continental conditions. Indeed, the observed associations between mycorrhizal fungi production and latewood width increased when the plot slope decreased, probably due to higher water or nutrient availability.

The relationships between mycorrhizal fungi production and latewood formation may be disguised by several reasons. First, fungi species may show contrasting associations with their hosts, similarly to the observed greatly variable responses to climate conditions (e.g. Boddy et

al., 2014). Second, host activity may influence mycelium production rather than mushroom fruiting, while the relationships between them remains broadly uncertain, and multiple environmental and biotic factors may affect fungi fruiting (Diez et al., 2013). Third, even though mycorrhizal fungi gain carbon mainly from their hosts, they may also obtain carbon by decomposing soil organic matter (Talbot et al., 2008). Therefore, significant relationships between fungi production and tree growth are difficult to find, probably because of the complex links existing between environmental constraints, mushroom production and tree growth phenology (Büntgen et al., 2013). Consequently, although we did not find significant associations in all the study plots, our results are a valuable contribution in the understanding of the long-term relationships between tree growth and fungi production.

To conclude, our findings indicate that latewood variables from tree species located in forests subjected to seasonal summer drought presents linkages with fungal yields in Mediterranean pine forests. Therefore, latewood production is a promising proxy of fungal yield in drought-prone forests. Further research is required to disentangle the links between climate, tree growth and mushroom production including seasonal assessments of wood formation, carbon use and changes in biomass of the soil mycelium.

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SUPPLEMENTARY MATERIAL

Linkages between climate, seasonal wood formation and mycorrhizal mushroom yields

Irantzu Primicia, J. Julio Camarero, Juan Martínez de Aragón, Sergio de-Miguel and José Antonio Bonet

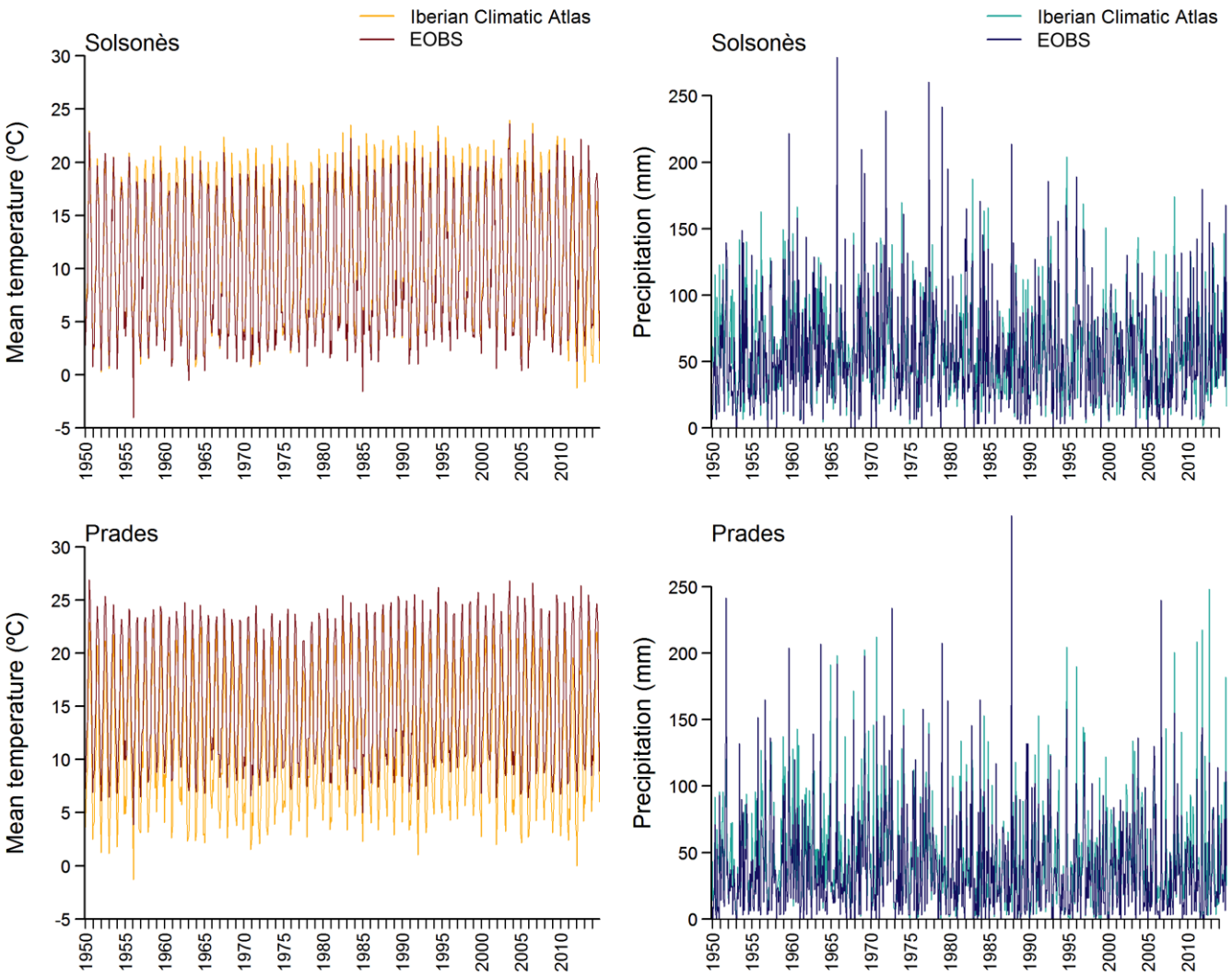
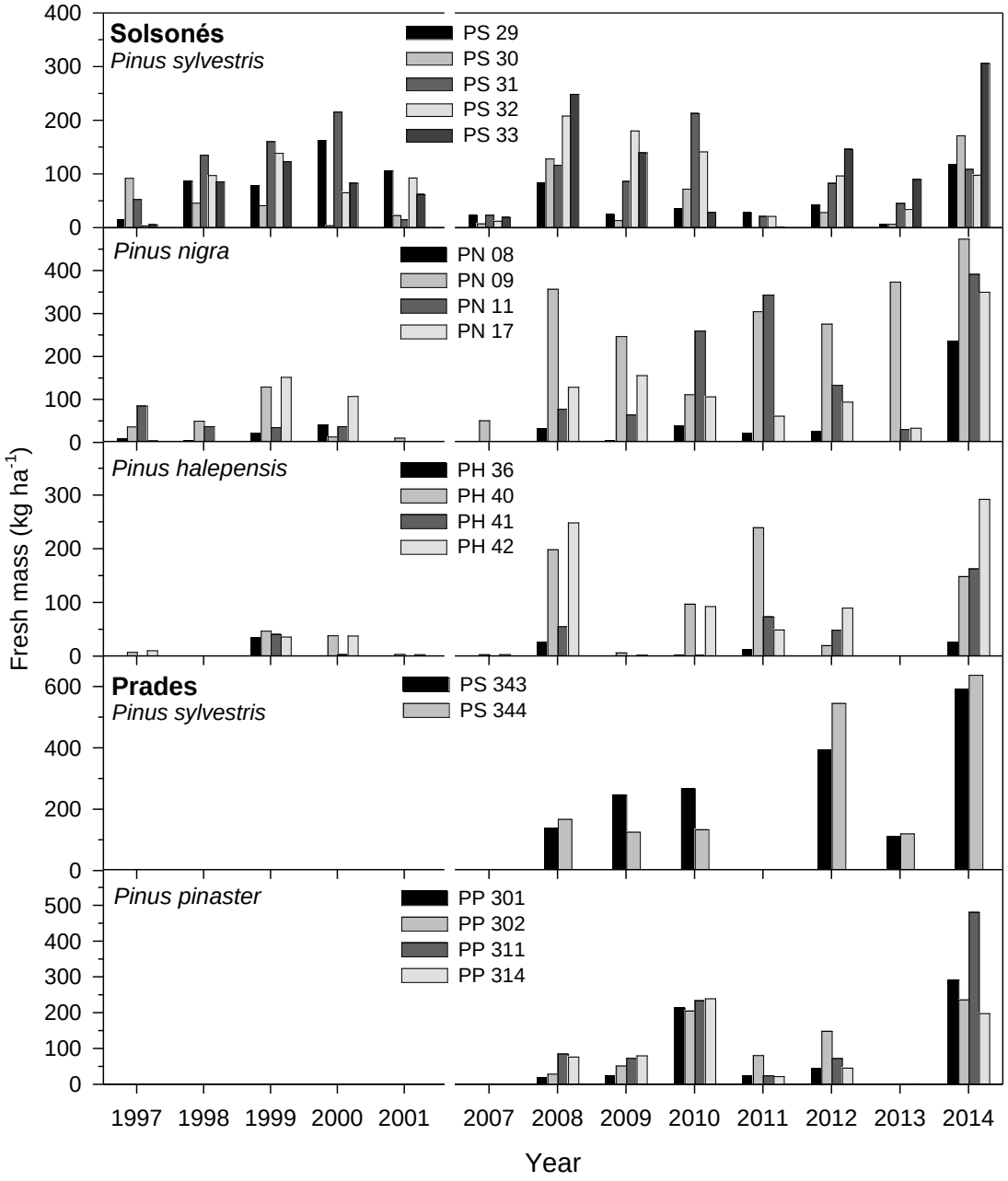


Figure A1. Mean annual temperature and annual precipitation recorded in the two study areas (Solsonès, Prades) and considering the 1950-2014 period. Compared data correspond to the Iberian Climatic Atlas (Ninyerola et al., 2005) and the European E-OBS 0.25º-gridded (Haylock et al., 2008) data sets.



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557 **Figure A2.** Mean annual mycorrhizal mushroom yield data recorded in five pine species

558 from the two study areas. Pine species abbreviations: PS: P. *sylvestris*, PN: *P. nigra*, PH: *P.*

559 *halepensis*, PP: *P. pinaster*.

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562 **Table A1.** Ten most abundant fungal species (kg ha^{-1} yr^{-1}) recorded in each study site

563 considering different pine species.

Site		Pine species	Fungal Species
Solsonès	Sols onès	Scots pine , *Pinus sylvestris*	*Tricholoma fracticum* (Batsch) Kreisel, *Suillus variegatus* (Swartz) Rich. & Roze., *Suillus luteus* (L.) Roussel., *Hydnum repandum* L., *Russula torulosa* Bres., *Hygrophorus latitabundus* Britz., *Lactarius deliciosus* (L.) S. F. Gray, *Hebeloma edurum* Métrod ex M. Bon, *Suillus collinitus* (Fr.) Kuntze, *Lactarius sanguifluus* (Paul.) Fr.
		Black pine, *Pinus nigra*	*Chroogomphus rutilus* (Sch.) Miller, *Suillus granulatus* (L.) Roussel., *Tricholoma fracticum* (Batsch) Kreisel, *Hygrophorus latitabundus* Britz., *Cantharellus lutescens* Fr., *Lactarius deliciosus* (L.) S. F. Gray, *Suillus collinitus* (Fr.) Kuntze, *Amanita ovoidea* (Bull.) Link., *Paxillus atrotomentosus* (Batsch) Fr., *Suillus luteus* (L.) Roussel.
		Aleppo pine, *Pinus halepensis*	*Hydnum repandum* L., *Hygrophorus latitabundus* Britz., *Tricholoma fracticum* (Batsch) Kreisel, *Tricholoma caligatum* (Viv.) Ricken., *Cantharellus lutescens* Fr., *Russula sanguinea* (Bull. ex St. Amans) Fr., *Lactarius deliciosus* (L.) S. F. Gray, *Suillus collinitus* (Fr.) Kuntze, *Suillus granulatus* (L.) Roussel., *Lactarius chrysorrheus* Fr.
Solsonès	Prades	Scots pine , *Pinus sylvestris*	*Lactarius vellereus* (Fr.) Fr., *Russula chloroides* (Kromb.) Bres., *Lactarius chrysorrheus* Fr., *Lactarius deliciosus* (L.) S. F. Gray, *Russula delica* Fr., *Ramaria aurea* (Sch.) Quél., *Macrolepiota procera* (Scop.) Sing., *Lactarius violascens* (Otto) Fr., *Mycena zephirus* (Fr.) Kumm., *Russula sanguinea* (Bull. ex St. Amans) Fr.
		Maritime pine, *Pinus pinaster*	*Suillus granulatus* (L.) Roussel., *Lactarius vellereus* (Fr.) Fr., *Macrolepiota procera* (Scop.) Sing., *Tricholoma terreum* (Sch.) Kumm., *Chroogomphus rutilus* (Sch.) Miller, *Leucopaxillus gentianeus* (Quél.) Kotl., *Lactarius vinosus* Quél, *Rhodocollybia butyracea* (Bull.) Kumm., *Mycena seynesii* Quél., *Lactarius deliciosus* (L.) S. F. Gray

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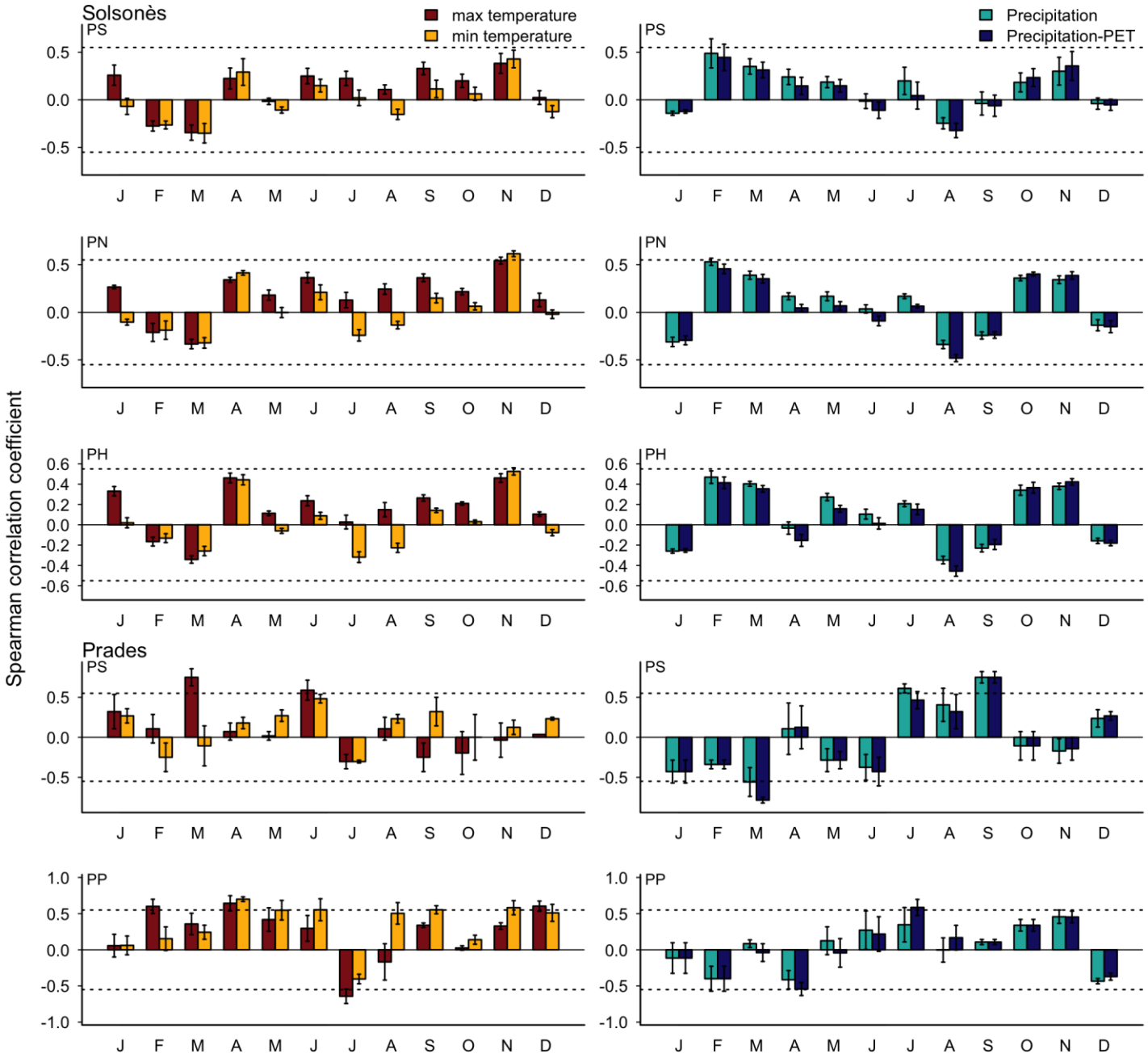
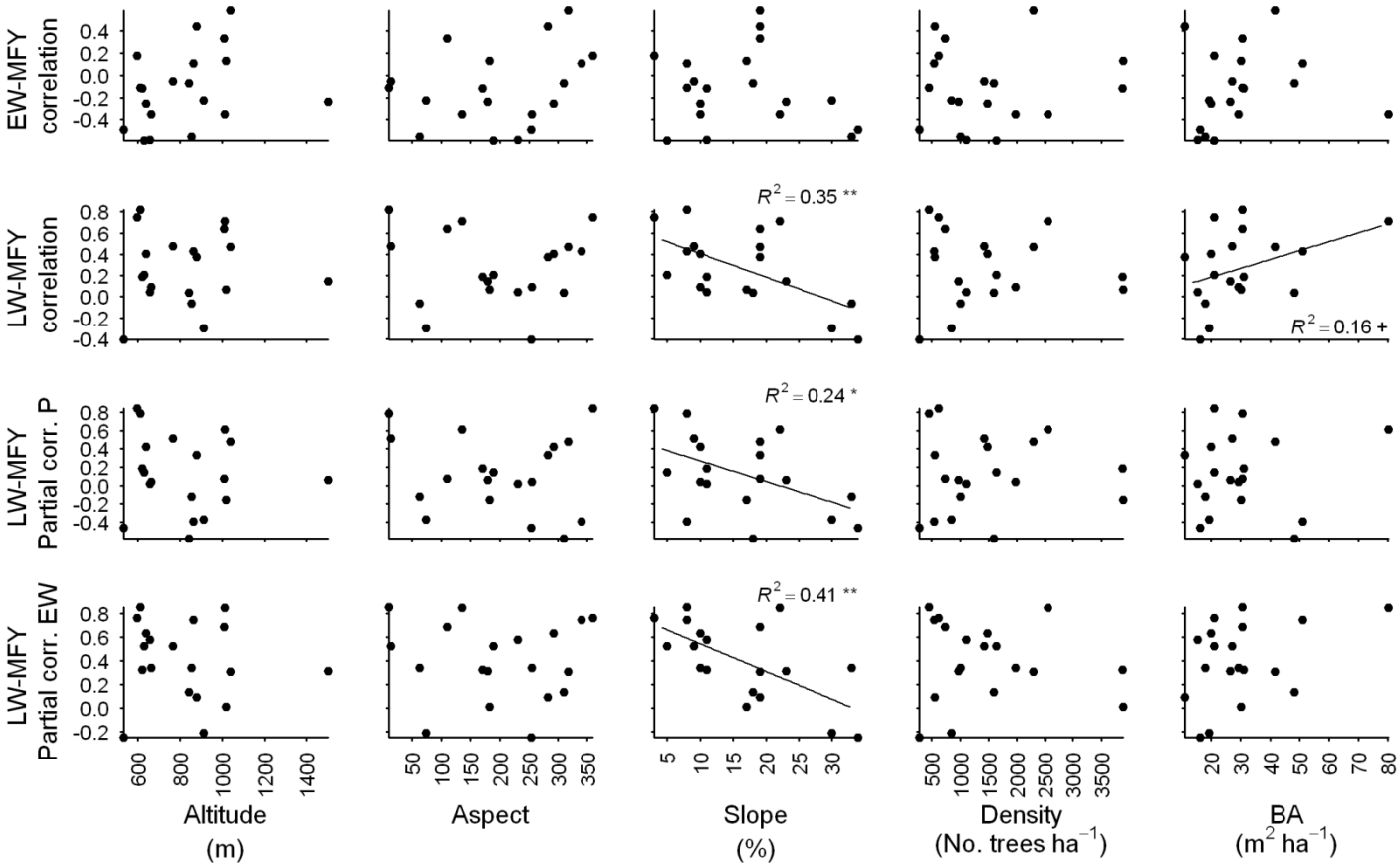


Figure A3. Correlations (Spearman coefficients) obtained by relating between mean annual saprotrophic fungi yield and monthly minimum and maximum temperature, precipitation, and water balance (precipitation minus potential evapotranspiration, PET) variables for each tree species and sample site. Horizontal dashed lines represent $P < 0.05$ significance levels. Pine species abbreviations are as in Figure A2.



573 **Figure A4.** Linear relationships (Spearman correlation coefficients) between earlywood
574 (EW) and latewood widths (LW) and mean annual mycorrhizal fungi yield (MFY), and partial
575 correlations calculated between LW and MFY by controlling for climatic (cumulative
576 precipitation from August to September- P) or growth effects (EW) and plots characteristics.
577 Abbreviations: BA, basal area. Significance levels: *$P \leq 0.05$; **$0.05 < P \leq 0.01$; ***$0.01 < P \leq$
578 0.001

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